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Life History and Immature Stages of the Bee *Neofidelia* (Hymenoptera, Fideliidae)

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ABSTRACT

The mature larva, pupa, and biology of the Chilean bee *Neofidelia profuga* Moure and Michener are described and compared with those of the South African *Fidelia villosa* Brauns. Although a number of interesting differences occur between these two species, they share numerous similarities. The information on the biology and immature stages of *Neofidelia profuga* supports the conclusion, presented in a previous paper, that the family Fideliidae and the leaf-cutter bee family Megachilidae are related.

RESUMEN

Se describen la larva madura, la pupa, y la biología de la abeja chilena *Neofidelia profuga* Moure y Michener, y se les compara con las de la especie sudafricana *Fidelia villosa* Brauns. Aunque existen numerosas diferencias interesantes entre estas dos especies también hay numerosas semejanzas. Los datos sobre la biología y los estadios larval y pupal de *Neofidelia profuga* confirman la conclusión, presentada en trabajo anterior, de que las familias Fideliidae y Megachilidae están relacionadas.

INTRODUCTION

In this paper I describe the mature larva, pupa, and biology of *Neofidelia profuga* Moure and Michener and compare them with those of *Fidelia villosa* Brauns. These species belong to the Fideliidae, the smallest family of bees, which contains three genera and a handful of species. The

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family has a disjunct, Southern Hemisphere distribution, with *Fidelia* and *Parafidelia* in arid parts of southern Africa and with two species of *Neofidelia* (*profuga* and *longirostris* Rozen) on the southern approaches to the Atacama Desert of Chile.

I (Rozen, 1970) reviewed the systematic and phylogenetic knowledge of the family and presented for the first time information on the nest structure, development, and immature stages of *Fidelia villosa*.¹ Many similarities of the Fideliidae to the Megachilidae in biology, larval structure, and adult anatomy were demonstrated, and I concluded that most of these features must have stemmed from the common ancestor of the two. The present paper is a continuation of the inquiry into the systematic and phylogenetic relationships of the family to other families of bees and into the interrelationships within the Fideliidae.

The field work that led to the present paper was accomplished with the able assistance of Señor Luis E. Peña G., Santiago, Chile. Dr. Andrew R. Moldenke (University of California, Santa Cruz), Professor Haroldo Toro (Universidad Católica, Valparaíso, Chile), and Mr. James H. Hunt (University of California, Berkeley) accompanied me in Chile during the investigations and assisted in the search for nest sites. Miss Liliane Flöge prepared the dissections and drawings of immature stages, and Mrs. Marjorie Favreau diagramed the burrows.

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BIOLOGY

DESCRIPTION OF NESTING SITE: A number of nesting areas of *Neofidelia profuga* were discovered. A site with a few widely scattered burrows was observed at Llano de Higuera, Coquimbo Province, Chile, October 15, 1971. Two moderate-sized nesting areas adjacent to each other in Quebrada San Carlos (fig. 1) near Vicuña, Coquimbo Province, were studied October 17, 1971, at which time most details of nest structure were recorded and young larvae and eggs recovered. A large site at Pajonales, Atacama Province (fig. 2) was briefly excavated on October 19, 1971, and numerous cocoons containing live larvae and parasites were collected. All sites, essentially identical, were situated in broad washes of a low gradient or, at Pajonales, on or near a gently sloping, unused dirt roadway. The sites were not significantly different in general aspect from the nesting

¹Cockerell (1933) gave some data on the flight and digging habits of females at a large nesting area near "Calvinia, in a dry region of South-West Africa" (almost certainly an error for Calvinia, Cape Province, Republic of South Africa).



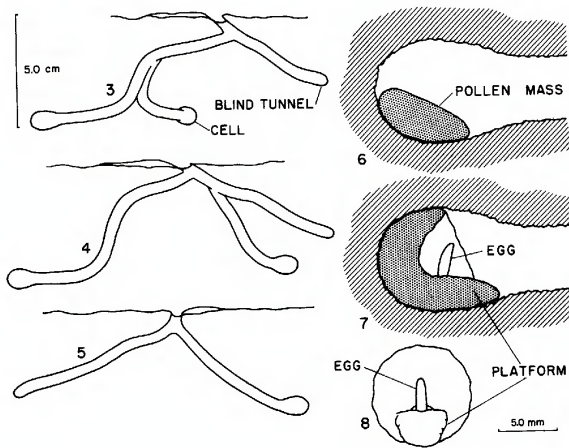
FIGS. 1, 2. Nesting sites of *Neofidelia profuga*. 1. At Quebrada San Carlos near Vicuña, Coquimbo Province, Chile. Almost the entire bare area was occupied by nesting females. 2. At Pajonales, Atacoma Province, Chile. Most nests were scattered along barren strip extending to middle of photograph.

area of *Fidelia villosa* 30 miles southeast of Keetmanshoop, South-West Africa (Rozen, 1970). Rains are infrequent throughout the range of *N. profuga* and consequently nests were in little danger of moisture at the cell level during the nesting season, which occurred during the dry period. Apparently rains are rarely sufficiently abundant to wash cocoons out of the ground at other times of the year.

All areas were desert scrub with scattered thorny plants and cacti. Most *Neofidelia* at Llano de Higuera were associated with a large cactus belonging either to the genus *Trichocereus* or *Eulychnia* which occurred sporadically over much of the area. A similar cactus was found adjacent to the nesting area at Quebrada San Carlos and almost certainly was the main source of food there. The pollen plant at Pajonales was *Calandrinia* (Portulacaceae), the dominant plant; it covered vast stretches including the nesting area.

The few nests discovered (two excavated) at Llano de Higuera were in sand, which at the cell level was somewhat compact and lacked visible signs of moisture. The larger nesting aggregation, consisting of more than several dozen burrows, at Quebrada San Carlos (fig. 1), was about 10 meters long and 2 to 3 meters wide. The soil was loose, dry, coarse sand and gravel to the depth of the cells. The smaller aggregation, about 100 meters away, was in fine sand which was dry and compact a few centimeters below the surface. Only six nests were found here, all in a meter square. The nesting area as well as the size of the population at Pajonales was extensive, with many hundreds of males and females at the flowers. Nests tended to be concentrated in places along the roadway where the soil was moderately hard and dry and contained no large stones or gravel. In general, *N. profuga* seems to nest in loose aggregations, as was the case with *Fidelia villosa*.

NESTING ACTIVITY: At all sites, a nest entrance (figs. 3–5) consisted of an opening penetrating obliquely, usually toward the uphill side in situations where the ground was sloping. A large tumulus, perhaps 3 to 4 cm. long, extended from the side opposite the direction of the descending burrow. All active nests had open entrances, but the main tunnels were filled with loose soil below the entrance. Tunnels were normally 5 to 6 mm. in diameter, but in very loose substrate they were somewhat larger, presumably because pebbles or sand fell into the tunnels as the females excavated. The main burrow (figs. 3–5) descended obliquely, perhaps 20 to 30 degrees from the horizontal, and usually divided a few centimeters below the surface. Secondary tunnels were the same diameter as the main tunnel and descended in a meandering fashion at the same angle or at a greater angle. One of the secondaries usually branched again at a variable



FIGS. 3-8. Nest components of *Neofidelia profuga*. 3-5. Diagrams of nests, lateral view. 6. Cell with provisions not shaped nor containing egg, lateral view. 7. Same except provisions shaped and egg inserted, lateral view. 8. Provisions and egg as viewed from cell opening.

Scales refer to figures 3-5 and 6-8, respectively.

distance from the first ramification. At Quebrada San Carlos three nests (figs. 3, 4) each consisted of three rami; when first discovered, one nest was being closed by a female and therefore was presumably complete. Two other nests (fig. 5) had only two rami. At Llano de Higuera each of two nests was composed of a single tunnel extending to an incompletely provisioned cell. In all nests, branches were filled with loose soil although near the cells the tunnel may have been only partly filled. Walls of tunnels were not specially worked nor was any secretion applied to them. Tunnels were not constricted at cell entrances.

Cells at all sites were about 4.5 to 7.0 cm. deep, 11 to 15 mm. (five measurements) long and 9 mm. (three measurements) in maximum diameter. Each cell was unfilled with soil, essentially horizontal, and arranged singly. Without any special lining, cells were essentially a simple widening at the end of the burrows. Although cell closures could not be detected because of the loose nature of the tunnel fill, it seems unlikely that a plug of specially worked, compact soil would have gone unnoticed.

Not all branches of a nest ended in cells. In each of the three nests consisting of three rami at Quebrada San Carlos, one branch ended blindly, without a terminal widening and without provisions. In each of the two nests with two branches, one branch also ended blindly. The

occurrence of (1) a completed nest with three branches, one of which was blind, (2) two nests, each with two branches, one of which ended blindly, and (3) several nests, each consisting of a single tunnel and an incompletely provisioned cell tentatively suggests that completed nests may be composed normally of three branches and that the blind one is second in order of construction. It seems certain that the blind branch is an integral part of nest structure, for it was found in all nests consisting of more than a single burrow.

One female crawled for a considerable period of time around a nest entrance as she gathered material to fill in the opening. This activity apparently marked completion of the nest. Tumulus material as well as surface soil was used as fill; the tumulus was still somewhat in evidence after she had finished the closure.

Nesting sites both at Quebrada San Carlos and at Pajonales had been active in previous seasons, as judged by numerous old cocoons.

Nests of *Neofidelia profuga* and *Fidelia villosa* share certain striking characteristics in addition to burrow size and cell size. Both have conspicuous tumuli, main burrows that angle into the ground, tunnels that branch, and cells that are horizontal and completely unlined. Furthermore, both genera construct blind tunnels, an unusual element in bee nests. Nest structures of the two genera differ, however, in some features: the cells of *N. profuga* are shallower; the cell diameter is distinctly wider than the tunnel diameter; there is generally (perhaps invariably) more than one cell to a completed nest. Furthermore, burrows of this species apparently ramify less, the ramifications occur close to the surface, and there is presumably only a single blind tunnel per nest.

PROVISIONING: *Neofidelia profuga* is polylectic; females carrying large quantities of dry pollen on their metasomal scopa have been collected both on *Calandrinia* and on *Trichocereus* (or *Eulychnia*). Pollen is not transported on the hind legs as had been once suspected for the African members of the family. The provisions are moistened (presumably with nectar) and deposited on the rear floor of the cell, as a flattened wafer (fig. 6). With its bottom conforming to the curvature of the cell floor, its flat top surface tilts somewhat toward the cell entrance. The pollen-nectar mass is moist but friable (i.e., not compact), both when incomplete and when complete. After the last pollen load is deposited, the female, probably with the aid of her modified pygidial area, forms the provisions into an unusual cup-shaped mass (figs. 7, 8) observed in scores of cells at Quebrada San Carlos and Pajonales. The provisions occupy the rear of the cell and extend from ceiling to floor, as diagramed. The female forms a large concavity on the exposed surface and constructs an irregularly shaped platform at

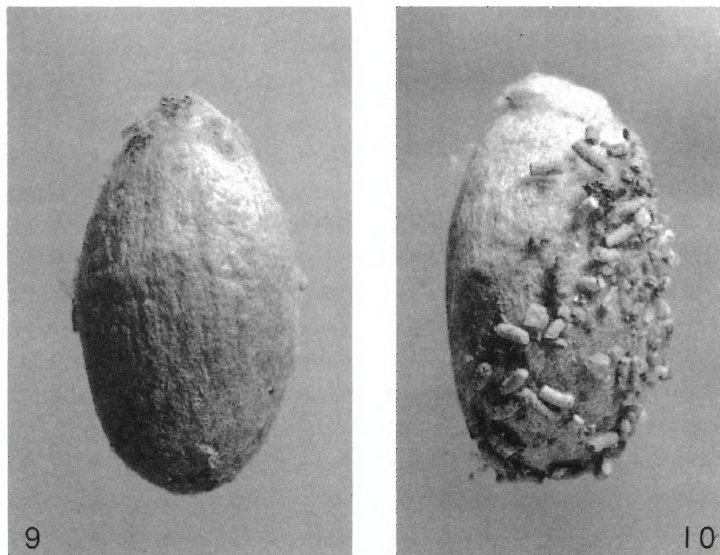
the bottom of the concavity. This platform extends beyond the rest of the provisions, and the egg, posterior end down, is shallowly embedded toward its rear. The erect egg tilts toward the cell opening and is exposed to the cell lumen. The provisions do not surround it, as they do in *Fidelia villosa* (Rozen, 1970, fig. 13).

DEVELOPMENT: The egg (figs. 7, 8) of *Neofidelia profuga* is semitransparent, whitish, slightly curved, has a smooth but not extremely shiny chorion, and is 3.1 to 4.0 mm. (four measurements) long and 1.0 to 1.1 mm. (three measurements) in maximum diameter. Its shape is unusual in that the anterior end is more pointed than the posterior. Just before eclosion, the chorion adheres to the body of the first instar which is able to move to and fro, and the larval tracheae fill with air. After the first instar hatches, it remains almost vertical with its posterior end shallowly embedded but its anterior end is capable of bending toward the cell opening so that the larva assumes a looped position while feeding on the pollen-nectar mixture of the platform (fig. 7) in front of it. It apparently maintains this position for the first stadium, but orientation and feeding actions of subsequent instars are not known. All larval instars are capable of vigorously wriggling and twisting their bodies, actions that enable them to shift position though seemingly in random directions. Larvae, which are hardy (several were transported by car and plane for weeks) like those of *Fidelia villosa*, quickly develop and the last instar (probably the fourth) is reached while the body of the larva is quite small and well before the provisions are even half consumed. The larva, like that of *F. villosa*, starts defecating dry yellow pellets as soon as it reaches the last stage. Hence fecal pellets can often be seen in conjunction with the stored provisions. Two fourth instar larvae from Quebrada San Carlos matured while I was in transit in Chile and Brazil. One had already spun a cocoon or at least a partial cocoon and the other had just started to spin when they were preserved on November 5, 1971. This indicates that larvae start cocoon spinning shortly after they are through feeding, as did *F. villosa*.

The process of cocoon spinning is similar to that of *Fidelia villosa* (Rozen, 1970) and the cocoon (figs. 9, 10) itself resembles that of *F. villosa*, with certain exceptions. The larva begins by spinning a webbing of fine brownish silk that forms a loose, soft, woolly mass that presumably occupies much of the cell; this webbing was not observed in *F. villosa*. Because of its soft texture, the fibrous material tends to be worn from some cocoons, particularly those that have been in the ground for more than a year. Adhering to the fibers are scattered fecal pellets and occasional sand grains. Within the mass the larva spins the solid part of its cocoon, which is an opaque, tan, oblong spheroid with a maximum diameter of 6 to 7 mm.

and an approximate length of 11 to 14 mm. The cocoon on *N. profuga* has a single nipple at the apex in contrast to the cocoon of *F. villosa* which has both ends nipped. The nipple of *N. profuga* is large, usually dimpled apically, and more loosely woven than the rest of the cocoon.

The thin outer layer of the cocoon consists of more or less appressed, partly adhering sheets of parchment-like fibers that together are dense.



FIGS. 9, 10. Cocoons of *Neofidelia profuga*. Nipped ends at top.

Although thin, this layer is thicker and more fibrous in appearance than the outer layer of the cocoon of *F. villosa*. The “glue” lines visible on the outside of the cocoon of *F. villosa*, cannot be seen on the cocoon of *Neofidelia profuga*. If the outer parchment-like layer is peeled away, the longitudinal “glue” lines, composed of brownish material presumably extruded from the anus, come into view on the outer surface of the middle layer of the cocoon. The most conspicuous element of the middle layer is sand which almost certainly is ingested and then defecated after most of the fibrous material of the cocoon has been discharged from the salivary glands. The sand layer differs from that of *F. villosa* as follows: (1) it is reddish tan rather than very dark brown (perhaps partly a result of the soil with which it is composed); (2) the sand grains are more irregular in size and are often larger; (3) it is thicker—0.3–0.4 mm.; (4) it seems to

have incorporated in it some fibrous material, presumably silk, that is spun while the larva defecates; (5) it is less brittle, tending to break like cardboard; and (6) it is less compact and the sand is not glued by glistening material. On the inside of the sand layer is a thin but distinct layer of woven material consisting of short fibers. This layer is not present in the cocoon of *F. villosa*.

As the adult bee emerges, it chews away much of the cocoon just behind the nipple so that the nipple is usually attached only by strands of the fibrous outer layer on a vacated cocoon. Within old cocoons are usually found soil, cast larval and pupal skins, and at the rear a quantity of caked white material adhering to the wall.

Six larvae collected as postdefecating forms in cocoons from Pajonales pupated in late November, 1971, and adults of four emerged and were killed December 3, 1971; the two other pupae, almost adults, were preserved the same day. These facts indicate that the pupal duration is short. Other postdefecating larvae collected from Pajonales remained dormant.

ADULT ACTIVITY: *Neofidelia profuga* mates both at the nesting site and at the flowers from which the females gather pollen. At the nesting site, mating is quick, accompanied by considerable tumbling on the ground. Males in search of females on the flowers fly swiftly from flower to flower. At Llano de Higuera males occasionally rested in cactus flowers and apparently waited for foraging females to land.

The sleeping habits of this species were not observed although females presumably spend the night in the ground. Rozen (1970) reported a male of this species sleeping in the flower of *Alona*.

Neofidelia profuga was active at all sites during the heat of the day. At Quebrada San Carlos females became active around 11:00 A.M. on a clear but relatively cool day.

Males of *N. profuga* when held occasionally attempted to pinch by curving their metasomas around my finger, much as has been described for *Fidelia villosa*. This behavioral character should again be checked for *N. longirostris*, because Rozen (1970) reported that the species did not pinch.

The hind basitarsus of females of both species of *Neofidelia* is very thin and has two rows of posteriorly directed hairs, so that the hairs, combined with the basitarsus, form a troughlike structure. Females of *N. profuga*, when backing out of the main tunnel during nest construction, push the earth backward with the front legs and, on emerging, flip the earth with the trough-like basitarsi. Hence, in spite of the dissimilar appearance of the basitarsi of *Fidelia* and *Neofidelia*, females of both genera use them for the same purpose and in a similar way. The motion of the leg of *Neofidelia*,

however, is probably back and forth, parallel to the long axis of the body rather than lateral flinging, characteristic of *F. villosa*.

PARASITISM: Parasitic bees were not seen at any of the nesting sites of *Neofidelia profuga*. Several young meloid larvae were recovered from cells at Quebrada San Carlos; one was embedded in a small cavity within the pollen mass itself. At Pajonales a number of cocoons, presumably with live occupants, were collected. The following tabulation of the contents of these cocoons may reflect something of the parasitism rate at the site although it should be borne in mind that obviously vacated cocoons were not collected to begin with:

Vacated or with dead <i>Neofidelia</i> adults	15 cocoons
Dead mutillid larva	1 cocoon
Live postdefecating <i>Neofidelia</i> larvae	12 cocoons
Live mutillid larvae	2 cocoons
Total	30 cocoons

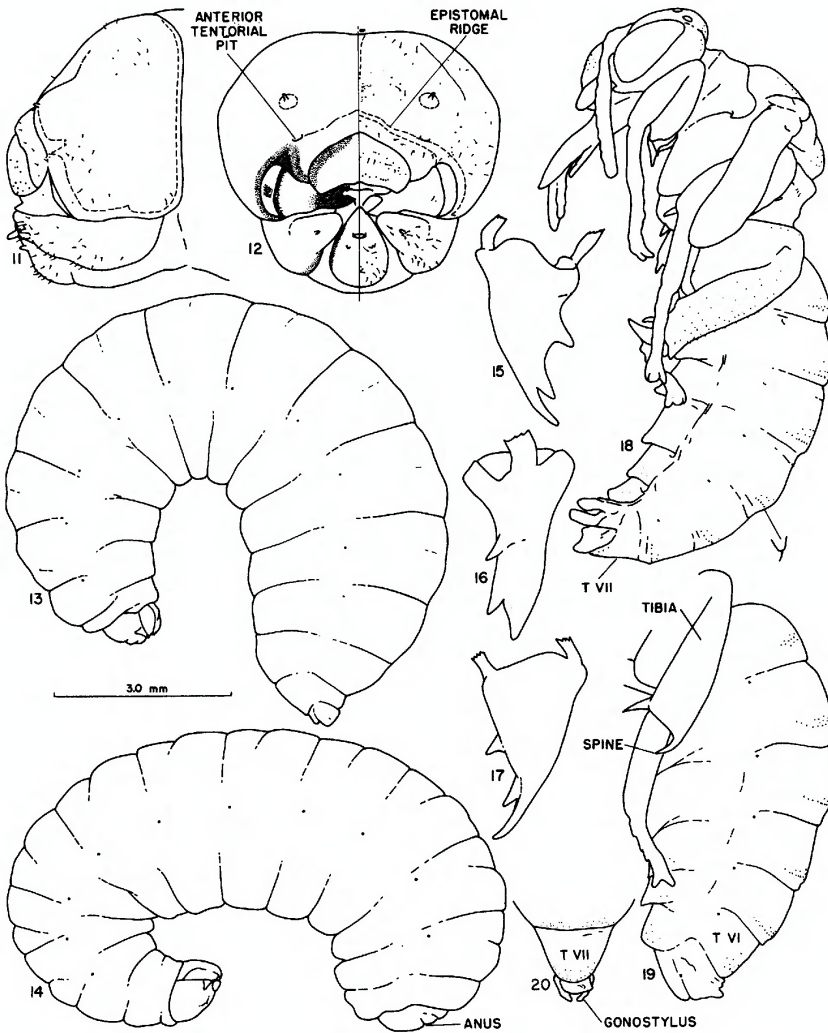
The larval mutillids had spun cocoons within the cocoons of *Neofidelia*. One adult male mutillid, a nocturnal form, emerged and was kindly identified by Mr. D. J. Brothers, University of Kansas, Lawrence, as "*Photopsis*" *gayi* Mickel. Three meloid larvae and one bombyliid larva, none enclosed in cocoons, were recovered from the site at Pajonales.

MATURE LARVA

Figures 11-17

DIAGNOSIS: The wider head, nonspiculate condition of the mouthparts, complete epistomal ridge, nonspiculate body integument, less conspicuous and more restricted body setae, easily distinguish the mature larva of this species from that of *Fidelia villosa*.

HEAD (FIGS. 11, 12): As seen from front, combined head capsule and labiomaxillary region (fig. 12) wider in relation to length than that of *Fidelia villosa*. In other respects, as described for *F. villosa* except for following: epipharynx, hypopharynx, dorsal surface, and much of basal part of maxilla and postmentum nonspiculate; pigmentation variable in intensity but distributed essentially as in *F. villosa*. Epistomal ridge developed not only below anterior tentorial pit but also moderately well mesiad of pits; external groove extending between anterior tentorial pits. Labrum more shallowly and broadly emarginate apically. Mandible (figs. 15-17) apically bidentate as in *F. villosa* but teeth apparently more sharply pointed although degree of pointedness may be variable and determined in part by abrasion; apical concavity perhaps less well-defined basally and with single large tooth dorsally; this tooth apparently variable in size. Labiomaxillary region only moderately produced, as seen in lateral view



FIGS. 11-17. Mature larva of *Neofidelia profuga*. 11. Head, lateral view. 12. Head, frontal view, left side of diagram showing patterns of pigmentation, right side showing distribution of sensilla and setae. 13. Larva starting to spin cocoon, lateral view. 14. Larva taken from cocoon, lateral view. 15-17. Right mandible, dorsal, inner, and ventral views.

FIGS. 18-20. Pupa of *N. profuga*. 18. Male, lateral view. 19. Female metasoma and hind leg, lateral view. 20. Male, apex of metasoma, dorsal view.

Scale refers to figures 13, 14, 18-20.

(fig. 11). Labial palpus and maxillary palpus subequal in size. Hypopharynx large and with lobes more distinctly separated than in *F. villosa*.

BODY: As described for *F. villosa* except for following: Caudal body annulets little, if at all, higher than cephalic ones; caudal annulets not slightly lower along median line than paramedially, hence not appearing as low paired tubercles. Integument nonspiculate; on specimen preserved before cocoon spinning, integument smooth and shiny; on specimens taken from cocoon, integument very wrinkled (more so than on *F. villosa*) and consequently dull; body setae (not illustrated) short and very sparse, becoming somewhat more dense at posterior end of body; setae much less conspicuous than on *F. villosa* and restricted dorsally to caudal annulets. Only outer half of spiracular atrium spinose; primary spiracular opening apparently without collar or with very shallow one, not guarded by spine; subatrium very short (about equal in length to atrium), composed of approximately two chambers. Tenth abdominal segment on specimen preserved before cocoon spinning moderately short with anus dorsal (and with rectal area partly extruded) but apparently not with dorsal part elevated, as described for *F. villosa* (elevation in *F. villosa* possibly artifact of preservation); tenth segment on specimen taken from cocoons shorter than on other specimen, hence similar to condition described for *F. villosa*. Imaginal disk of male genitalia, as described for *F. villosa*, not known for female in either species.

MATERIAL STUDIED: One mature larva, starting to spin, Quebrada San Carlos, near Vicuña, Chile, collected October 17, 1971, preserved November 5, 1971 (J. G. Rozen); one mature larva, same data, except collected as young larva October 17, 1971, taken from cocoon and preserved November 18, 1971; one mature larva, same data, except Pajonales, Atacama Province, Chile, collected in cocoon October 19, 1971, preserved February, 1972.

PUPA

Figures 18–20

DIAGNOSIS: The very short, fine setae (easily overlooked on first examination), absence of mesoscutellar tubercle, and the small tubercles on tergum VII of the male and VI of the female will serve to differentiate this pupa from that of *Fidelia villosa*. The male pupae of the two species can be easily recognized on the basis of the hind legs and gonostyli.

Length of male 8.0 mm., of female 7.0 mm.; body moderately straight so that tip of tongue not nearly touching tip of metasoma.

HEAD: As described for *Fidelia villosa* except for following: Integument of vertex and labioclypeal region with fine, very short setae. Gena with

small but distinct tubercle immediately behind base of mandible. Mandible of male apparently simple, gradually tapering to apex; mandible of female apparently with slight dorsal subapical bulge corresponding to subapical tooth of adult but not bidentate as in female of *F. villosa*.

MESOSOMA: As described for *F. villosa* except for following: Integument of mesoscutum and mesoscutellum with scattered, very short, fine setae; integument of hind leg, and especially of hind tibia, with short fine setae. Pronotum with lateral lobes somewhat produced in both sexes. Tegular tubercle apparently less conspicuous than that of *F. villosa*; mesoscutellum without distinct tubercle although on female median area of scutellum perhaps slightly raised. Prothoracic leg of male not modified as in *F. villosa*; profemur with small basal tubercle; hind leg of male modified in correspondence with modifications of adult; coxae of all legs each with moderate-sized apical tubercle; trochanters of all except hind legs of male with small but distinct apical tubercle; condition on hind trochanter of male unknown; hind tibia (fig. 19) of female with curved dorsal apical spine which encloses hairs of adult.

METASOMA: As described for *F. villosa* except for following: Terga I to VII of male and I to VI of female with apical bands of small tubercles, most of which bear short sharp-pointed setae; external sterna of female and apparently also of male protruding apically along median line and some bearing small, fine setae; metasomal tergum VII of male (fig. 20) entire, without apical spines; sternum VII of male not produced laterally and gonostyli small compared with those of *F. villosa*.

MATERIAL STUDIED: One male, one female pupa, Pajonales, Atacama Province, Chile, collected as larva October 19, 1971, pupa preserved December 3, 1971 (J. G. Rozen and L. Peña).

The pupa of the species is quite similar to that of *Fidelia villosa*. Contrary to an erroneous statement in Rozen (1970, p. 21) megachilid pupae (*Megachile*, *Heterostelis*, *Odontostelis*, and *Osmia*) known to me do not have tegular or mesoscutellar tubercles and they thereby differ from the pupae of *Fidelia* which have such tubercles. The pupa of *Neofidelia* has tegular tubercles but no mesoscutellar tubercles, and agrees with the pupae of known megachilids (except apparently for *Heterostelis*, Thorp, 1966) in that it has setae (though very short ones) on the vertex, scutum, and other areas of the body.

DISCUSSION AND CONCLUSIONS

The preceding account of the biology and immature stages of *Neofidelia profuga* attempts to contrast this species with *Fidelia villosa*. In spite of numerous interesting differences between the two species, one cannot help

being impressed with the great number of similarities they share. Agreement in provisioning, nest construction and structure, larval behavior, and anatomical features of larvae and pupae emphasizes the homogeneity of the family. All known features of *N. profuga* support the systematic relationships discussed by me (Rozen, 1970) of the Fideliidae to the Megachilidae, and the presence of body setae on the pupa adds even greater strength to these relationships.

Neofidelia profuga and *Fidelia villosa* nest only in xeric areas and their unlined cells suggest that they are restricted to such places because moist conditions during nesting would lead to liquefaction of the cell provisions and cause the death of the immature bee. If all fideliids lack cell lining, how can the disjunct present-day distribution of this family be accounted for? It seems unlikely that arid lands extended continuously from Chile to southern Africa after the separation of South America and Africa or even that arid "steppingstones" could have provided a bridge through time from one area to the other. Hence, it would seem that the family Fideliidae arose before the continents separated. Present geological evidence indicates that South America and South Africa began to divide approximately 80 million years ago during the Early Cretaceous and separated further in Late Cretaceous. The suggestion is then that the fideliids extend back to Cretaceous times. If this is true, then they are an old family, for the first bees could not have appeared before the Cretaceous because that is when pollen-bearing plants, the food source for all bees, first evolved.

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